Persist or produce: a community trade-off tuned by species evenness

KEYWORDS:
biodiversity, competition systems, demographic stochasticity, ecosystem functioning, niche theory, species coexistence

List of elements: manuscript, color version of figures 1-3; mono version of figure 4

Online enhancements: online appendices A-F; online tables A1-A2; online figures C1-C35 and D1-D9

Submitted as an article

Abstract

Understanding the effects of biodiversity on community persistence and productivity is key to managing both natural and production systems. Because rare species face greater danger of extinction, species evenness, a measure of how similar abundances are across species in a community, is seen as a key component of biodiversity. However, previous studies have failed to find a consistent association of species evenness with species survival and biomass production. Here, we provide a theoretical framework for the relationship among these three elements. We demonstrate that the lack of consistent outcomes are not idiosyncratic artifacts of different studies, but that it can be unified under one common framework. Applying a niche theory approach, we confirm that under demographic stochasticity evenness is a general indicator of the risk of future species extinctions in a community, in accordance with the majority of empirical studies. In contrast, evenness cannot be used as a direct indicator of the level of biomass production in a community. When a single species dominates, as expressed by the constraints imposed by the population dynamics, biomass production depends on the niche position of the dominating species, and can increase or decrease with evenness. We demonstrate that, high species evenness and an intermediate level of biomass production is the configuration that maximizes the average species survival probability in response to demographic stochasticity.

Introduction

Biodiversity is a central concern in conservation, in part due to its relationship with ecosystem processes such as biomass production (Margalef, 1963; Odum, 1969; Tilman et al., 1996; Chapin et al., 2000; Loreau, 2010; Vellend et al., 2013). This relationship has even generated interest as a means to augment biomass in production systems such as plantation forests (Erskine et al., 2006). However, biodiversity has traditionally been measured in these studies as species richness (Hooper et al., 2005), whereas the majority of species in a community are normally found to occur in low abundance, with only a few being extremely common (Preston, 1948; Tokeshi, 1990; Chapin et al., 2000; Sugihara et al., 2003).

Because rare species might be more vulnerable to demographic stochasticity under environmental stress, an equally relevant index of biodiversity is species evenness, i.e., how similar abundances are across species (Margalef, 1968; Levins, 1968; Stirling and Wilsey, 2001; Odum, 1969; Chapin et al., 2000). Further, species evenness may respond more rapidly to environmental changes than does richness (Chapin et al., 2000), so researchers have hypothesized that changes to species evenness may be a good indicator of the risk of future species extinctions in a community (Odum, 1969; Chapin et al., 2000; Halloy and Barratt, 2007). This hypothesis has also been supported experimentally by several studies (see table A1, available online)

Despite its potential utility as a measure of ecosystem state, research testing the influence of species evenness on ecosystem functioning has found more variable results than those for richness (Hillebrand et al., 2008), though the majority of these have been positive (see table A2, available online). Although positive effects of species evenness on biomass production have been shown both theoretically (Nijs and Roy, 2000) and empirically

(Wilsey and Potvin, 2000) (see table A2, available online), abiotic drivers of evenness (or of its reciprocal, dominance) may reverse this relationship (Mulder et al., 2004). For example, abundant resources can promote competitive dominance by a few species, and lead to reduced species richness and higher growth rates (Laliberté et al., 2013), in accordance with theory (Huston, 1979). When abiotic stress subsequently reduces this dominance, the resulting increase in evenness may be associated with lower biomass production (Wardle et al., 1997). Theoretical (Norberg et al., 2001) and experimental (Wittebolle et al., 2009) results suggest that systems with low species evenness may be less resistant to stress induced by environmental change. This suggests that there may be an intricate balance between competition (via its effect on species evenness), community persistence, and ecosystem functioning. Yet the nature of this relationship remains a major conceptual challenge (Wittebolle et al., 2009).

Given the prominent role of species evenness in both the persistence and productivity of communities, we build a conceptual framework based on niche theory whereby these axes can be viewed simultaneously, with the hope that this approach will shed light on apparently contradictory results. Our aim is to study the relationship among these three properties under a Lotka-Volterra framework and under the constraints imposed by the differential equations describing the population dynamic. In particular, to estimate species survival probability, we assumed stochastic noise in the demographic parameters. While our approach is focused exclusively on the relationship between community evenness and species survival probability, we also search for general patterns of context dependency, by examining the conditions under which a competition hierarchy would be expected to generate a trade-off between productivity and evenness, rather than a positive relationship between these two ecosystem measurements.

The paper is organized as follows. Firstly, we explain our theoretical framework based on niche theory. Secondly, we explain how we calculate species evenness, community biomass, the average survival probability of species under stochastic noise in demographic parameters, and the link among the three of them. Thirdly, we explain how to disentangle the role played by species evenness and biomass production in shaping species survival probability under demographic stochasticity. Finally, we explore the outcomes of our framework and discuss their implications.

Methods

Theoretical framework

Our theoretical framework of population dynamics is based on the generalized Lotka-Volterra competition model derived from niche theory (MacArthur and Levins, 1967; Levins, 1968; Svirezhev and Logofet, 1983; Logofet, 1993; Loreau, 2010; Saavedra et al., 2014). Mathematically, the dynamical model is given by

$$\frac{dN_i}{dt} = \frac{r_i}{K_i} N_i \left(K_i - \sum_{j=1}^{S} \alpha_{ij} N_j \right), \tag{1}$$

where variable $N_i \geq 0$ denotes the biomass of species i. The parameters are: $r_i > 0$ represents the growth rate of species i, $K_i > 0$ indicates the carrying capacity of species i (i.e., the biomass at equilibrium in monoculture), and $\alpha_{ij} \geq 0$ indicates the niche overlap between species i and j, which gives the competitive effect of species j on species i.

Assuming a D-dimensional niche space and that each species' niche is represented by a multivariate Gaussian-like function, the niche overlap between two species (α_{ij}) can be expressed as a function of their distance in the niche space (MacArthur and Levins, 1967;

Levins, 1968; Svirezhev and Logofet, 1983; Logofet, 1993):

$$\alpha_{ij} = e^{-d_{ij}^2/4\sigma^2}, \tag{2}$$

where σ is the niche width (assumed to be the same for all species and in all the D-dimensions of the niche space), and d_{ij} is the distance between species i and species j. The pairwise niche distances are computed by $d_{ij} = \|\boldsymbol{\mu}_i - \boldsymbol{\mu}_j\|$, where the vector $\boldsymbol{\mu}_i$ gives the position of species i in the niche space. By definition, we have $\alpha_{ii} = 1$, so that in the absence of pairwise niche overlap (or equivalently when species are in monoculture), each species reaches its own carrying capacity at equilibrium (Levins, 1968).

Note that without loss of generality, we can rewrite Equation (1) in the form: $dN_i/dt = N_i \left(r_i - \sum_j A_{ij}N_j\right)$, where A_{ij} is the competition strength matrix and is linked to the niche overlap matrix by $A_{ij} = r_i/K_i \cdot \alpha_{ij}$. The matrix A_{ij} is in general asymmetric (because the r_i and the K_i are different among species) and expresses the per capita effect of species j on the per capita growth rate of species i. The elements of the niche overlap matrix α_{ij} are dimensionless, while the competition strength has units $\text{time}^{-1}\text{biomass}^{-1}$ or $(\text{time}^{-1}\text{abundance}^{-1})$. This expression can be generalized, without changing qualitatively the results to incorporate species dependence on the width and amplitude of the niche curve (appendix B, available online).

Importantly, a niche-based competition model has two advantages for a theoretical framework, one technical and one conceptual (Case, 1990). The technical advantage is that in a Lotka-Volterra model (equ. 1) based on a competition matrix ($\boldsymbol{\alpha}$) derived from a niche space (e.g., equ. 2), the trajectory of the dynamical system will converge to a unique globally stable equilibrium point (independent of the initial conditions). This is the consequence of niche overlap matrix being inevitably *Volterra*-dissipative (Volterra, 1931; Svirezhev and Logofet, 1983; Logofet, 1993). Therefore, if one randomly generates an interaction matrix $\boldsymbol{\alpha}$ by sampling randomly the niche positions and then computing the pairwise niche overlap elements, the biomass values at equilibrium are only dictated by the carrying capacities and not by the intrinsic growth rates (Saavedra et al., 2014), and that equilibrium point is globally stable. In contrast, if one generates a competition matrix by drawing directly the niche overlap at random, then the global stability property is not anymore granted. The conceptual advantage is that by calculating the competition coefficients derived from a niche overlap framework, rather than drawing them directly at random, one can provide a clear biological and mechanistic interpretation based on competition for common resources.

Species evenness

Species evenness is a measure of how equally biomass is distributed among species in a given community. Traditionally, species evenness is calculated as the Shannon index by

$$J = -\frac{\sum_i p_i \log p_i}{\log S}, \tag{3}$$

where $p_i = N_i^* / \sum_j N_j^*$ is the fraction of species i's biomass (from the total biomass in the community) and S is the total number of species in the community. Species evenness, defined for $S > 1$, takes values in $[0, 1]$, where a value of one indicates that all species are equally abundant and a low value indicates that the community is dominated by few or a single species.

Community biomass

In the presence of interspecific competition, the total biomass of a community at the steady state of a Lotka-Volterra model (Equ. 1) is less than the sum of all the carrying capacities of the constituent species. The ratio between the total biomass at equilibrium and the sum of all carrying capacities can be used as a proxy for the relative biomass production in a community. This ratio is computed as:

$$P = \frac{\sum_i N_i^*}{\sum_i K_i}. \tag{4}$$

The ratio P is dimensionless and represents the fraction of potential biomass production achieved in the presence of interspecific competition. Our intent in using this ratio, rather than simply summed biomass, is to account for inherent productivity differences across communities, and thereby allow these results to be comparable across different distributions of species biomasses (Cardinale et al., 2006). For example, some species may naturally occur at low biomass because they have specialized niches, tend to occur in low-resource environments, or never achieve a large size. Increasing evenness may also appear to lead to an augmentation in biomass, simply because it involves an increase in the carrying capacity of species that have a low biomass. Our use of relative biomass therefore measures the competition-limited biomass of such species relative to their biomass in the absence of competition, and is akin to the measure used to assess over-yielding (the change in biomass beyond that obtained by each species in isolation) in biodiversity-productivity studies (Loreau, 1998; Hector and Bagchi, 2007; Cardinale et al., 2006).

Average survival probability of species under demographic stochasticity

To obtain an estimation of the survival probability of any species in a community, we calculated the average fraction of surviving species under demographic stochasticity. Specifically, for a given community represented by a niche overlap matrix ($\boldsymbol{\alpha}$) and a given biomass distribution $\boldsymbol{N}^*$, this average survival probability is calculated in the following way:

First, given $\boldsymbol{\alpha}$ and $\boldsymbol{N}^*$, we compute the corresponding vector of carrying capacities by $\boldsymbol{K} = \boldsymbol{\alpha} \cdot \boldsymbol{N}^*$. This vector of carrying capacities is the one that makes the Lotka-Volterra model (equ. 1) converge to the biomass distribution $\boldsymbol{N}^*$ at equilibrium. Our theoretical framework assumes that the biomass distribution, the niche overlap matrix, and the carrying capacities are constrained by the equation for the community dynamics.

Second, we mimic demographic stochasticity by introducing random and proportional variations to the calculated vector of carrying capacities $\boldsymbol{K}$. This is done by multiplying each of the vector elements by a log-Normal random number of mean 0 and standard deviation of 0.3, 0.1, and 0.01 for a high, medium, and low level of environmental stochasticity, respectively. Note that this simulated environmental stochasticity on the carrying capacities is equivalent to simulated stochasticity on the intrinsic growth rate, as the carrying capacity in a competitive framework is given by the ratio between the intrinsic growth rate and the fixed intraspecific competition.

Finally, using these perturbed vectors of carrying capacities, we computed the fraction of surviving species at the steady-state of the Lotka-Volterra model (equ. 1). To obtain an estimation of the average survival probability of species, we repeated steps two and three 200 times, and computed the average fraction of surviving species under demographic stochasticity.

Linking evenness, biomass production, and species survival probability

To study the theoretical link among species evenness, biomass production, and survival probability of species in any given community represented by a niche overlap matrix $\boldsymbol{\alpha}$, we took an approach of exploring as exhaustively as possible the biomass production-evenness space, and estimating the survival probabilities. This approach followed three steps:

First, we randomly generated the niche position of each species in a two dimensional niche space and computed the niche overlap matrix $\boldsymbol{\alpha}$ (equ. 2). The two coordinates of each species were sampled uniformly between 0 and 1. The niche width was chosen such that the average interspecific niche overlap was within the range $[0.05, 0.3]$. The results are qualitatively robust to changes in the dimension of the niche space (results not shown).

Second, because our aim is to study the association imposed by the Lotka-Volterra model of species survival probability with biomass production and species evenness for a fixed number of species S, we generated a full gradient of species evenness from almost 0 to 1. To achieve such a gradient we could have randomly sampled vectors of carrying capacities and then computed the biomass of the species at the equilibrium point of the Lotka-Volterra model. However, for many of these simulated vectors of carrying capacities, the equilibrium point would have few or many species extinct. Then, these vectors of carrying capacities leading to species extinction would need to be disregarded. This of course would represent a considerable amount of computational time. Therefore, to achieve our gradient of evenness efficiently from a computational perspective, we decided to first generate the distributions of biomass and then to compute their corresponding vector of carrying capacities (expressed by the equation $\boldsymbol{K} = \boldsymbol{\alpha} \cdot \boldsymbol{N}^*$).

These biomass distributions were sampled from a log-Normal distribution of location parameter 0 and scale parameter drawn uniformly between 0 and 5. Note that our biomass sampling procedure explores intensively the full domain of potential biomass distributions, and consequently the full domain in the parameter space of carrying capacity compatible with coexistence. Therefore, our findings are general because they do not depend on a specific parameterization of demographic parameters (Rohr et al., 2014). We sampled 20 thousand species biomass distributions.

Finally, for each niche overlap matrix ($\boldsymbol{\alpha}$) and each generated distribution of species biomass ($\boldsymbol{N^*}$), we computed the corresponding level of species evenness (equ. 3), relative biomass production (equ. 4), and average species survival probability under demographic stochasticity.

Feasibility analysis

To understand the role played by species evenness and biomass production in shaping the average species survival probability, we studied the feasibility domain of each simulated community (Svirezhev and Logofet, 1983; Logofet, 1993; Rohr et al., 2014; Saavedra et al., 2014, 2016a,b). In this context, the feasibility domain corresponds to the domain in the parameter space of carrying capacities compatible with the survival of all species, i.e., given $\boldsymbol{\alpha}$ it is the set of carrying capacities such that their equilibrium points under the Lotka-Volterra model (equ. 1) yield solutions where all species have a strictly positive biomass, $N_i^* > 0$. Outside this domain, there is no set of carrying capacities leading to the survival of all species. Mathematically, the feasibility domain is defined by:

$$D_F(\boldsymbol{\alpha}) = \{\vec{K} \in \mathbf{R}^S_{>0} | \text{ there exist } \vec{N}^* \text{ with } N_i^* > 0 \text{ such that } \vec{K} = \alpha \vec{N}^*\}. \qquad (5)$$

If one chooses a vector of carrying capacities ($\boldsymbol{K}$) inside that domain, then by definition, the Lotka-Volterra model (equ. 1) converges to a positive equilibrium point given by $\boldsymbol{N}^* = \boldsymbol{\alpha}^{-1}\boldsymbol{K}$.

The feasibility domain of a niche overlap matrix $\boldsymbol{\alpha}$ is geometrically represented by an algebraic cone in the space of carrying capacities (Svirezhev and Logofet, 1983; Logofet, 1993). A vector of carrying capacities close to its border is, by definition, more at risk of species extinction under demographic stochasticity. That is, the chances that a stochastic perturbation pushes the vector of carrying capacities outside the domain of feasibility (which implies at least one species going extinct) is larger for vectors closer to the border. Therefore, to increase the average survival probability, one possibility is to locate the vector at the center of the feasibility domain. Note that the geometric centroid of the cone describing the feasibility domain is one possible center. This geometric centroid, defined by the so-called structural vector $\boldsymbol{K}^{\boldsymbol{S}}(\boldsymbol{\alpha})$ (Rohr et al., 2014; Saavedra et al., 2014), can be computed based on the elements of the niche overlap matrix by the following formula

$$K_i^S(\boldsymbol{\alpha}) = \sum_{j=1}^{S} \frac{\alpha_{ij}}{\sum_{k=1}^{S} \alpha_{kj}}. \tag{6}$$

For any vector of carrying capacities $\boldsymbol{K}$, we calculate its deviation from the centroid $\boldsymbol{K}^{\boldsymbol{S}}(\boldsymbol{\alpha})$ by the angle between the two vectors (Rohr et al., 2014; Saavedra et al., 2014). This deviation is computed based on the scalar product:

$$\theta = \arccos\left(\frac{\sum_{i=1}^{S} K_i K_i^S}{\sqrt{\sum_{i=1}^{S} K_i^2}\sqrt{\sum_{i=1}^{S}(K_i^S)^2}}\right). \tag{7}$$

We stress that the notions of feasibility domain, structural vector, and deviation provide a mechanistic understanding of the dynamics of the community as whole, and are contained in the Lotka-Volterra model (equ. 1). The average survival probability cannot be deduced directly, but requires simulations and the addition of demographic stochasticity for its estimation.

Results

To explore the relationship among species survival probability, species evenness, and biomass production, we constructed randomly assembled communities of 10, 15, 20, 25, and 30 species. For each level of species richness, we generated communities with an average interspecific niche overlap within the range of $[0.05, 0.3]$. For other overlap values the results are qualitatively equivalent. For each niche overlap matrix, we sampled communities spanning the whole range of species evenness. Finally, for each generated community, we explored three levels of stochastic noise (standard deviation of 0.01, 0.1, and of 0.3) on the demographic parameters to estimate survival probabilities.

Species evenness and survival probability

We found a positive and strong relationship between the level of species evenness and the average survival probability of each species (fig. 1A). Note that the actual values of survival probability are completely dependent on the parameters used for the community and perturbations. Importantly, the level of random perturbations does not change the relationship between species evenness and survival probability, and this pattern is highly reproducible in simulated communities of different sizes and characterized by different average niche overlap (figs. C1-C15, available online). It is worth mentioning that an increase in the average niche overlap always results in an overall decrease of the average survival probability, keeping fixed the number of species and the level of demographic stochasticity (figs. C16-C20, available online). This negative relationship between niche overlap and survival probability is perfectly in line with previous studies showing that an increase in competition results in a decrease of the feasibility domain (Vandermeer, 1970; Bastolla et al., 2005; Saavedra et al., 2014). We also explored community evenness using the Simpson index (appendix D, available online), and the results are qualitatively equivalent. In general, these findings reveal that community evenness is directly and positively linked to the likelihood of species survival, providing a theoretical justification for the use of evenness as a proxy for the probability of future species extinctions under demographic stochasticity (Odum, 1969; Chapin et al., 2000; Halloy and Barratt, 2007).

Species evenness and biomass production

ontrast to the direct relationship between species evenness and survival probability, we found a multidirectional relationship between species evenness and relative biomass (fig. 1B). Figure 1B shows that at the maximum level of species evenness, relative biomass is at an intermediate level compared to its total possible range. When species evenness decreases from this maximum, relative biomass can either increase or decrease. Specifically, if the species that has the lowest average niche overlap with the other species (computed as $\bar{\alpha}_i = \frac{\sum_{j \neq i} \alpha_{ji}}{S-1}$) dominates the community, a decrease in species evenness implies an increase in relative biomass. Alternatively, if the dominating species has a high average niche overlap, the relative biomass decreases with declining evenness (fig. 1B). It can be mathematically proven that lower average niche overlap of the dominating species leads to large relative biomass, and vice versa (see appendix E for the mathematical proof, available online). This implies that species evenness cannot be used as a direct predictor of the relative biomass of a community. In a community dominated by a single species, the relative biomass depends on the niche overlap of the dominating species, and can thus increase or decrease with evenness. These results are robust to the change in species richness and average niche overlap (figs. C1-C15, available online).

The computer code for reproducing the simulations, especially for figures 1 and 4, is provided in the online appendix F.

Theoretical explanation for the link among evenness, biomass production, and survival probability

In this section, we first explain why the positive relationship between evenness and survival probability should be theoretically expected. Then we show how the deviation from the centroid of the feasibility domain of a community can be used to disentangle the relationship between species evenness and biomass production.

We start by providing an illustrated example of the feasibility domain and its implications for the average survival probability of species. Figure 2A represents the algebraic cone of the feasibility domain. Each axis corresponds to the carrying capacity values of a species (parameter space), which define the solution of the system (state space) (Svirezhev and Logofet, 1983; Logofet, 1993; Saavedra et al., 2016a,b). The cone is generated by the three blue vectors, which provide the limits of the feasibility domain. The dashed vector represents the centroid of the feasibility domain (the structural vector). Figure 2B shows a 2-dimensional slice of the cone in figure 2A. The outer triangle (gray) corresponds to the total domain of carrying capacities and is split in 7 domains. The inner triangle (red) corresponds to the feasibility domain where all three species survive (a larger feasibility domain indicates a greater range of parameters leading to a positive solution). In the other 6 domains, at least one species goes extinct. The identity of the surviving species is given by the number(s) inside the corresponding domain. Each blue dot at the border of the feasibility cone represents the limite at which one of the three species is fully dominating the system, the green symbol in the middle corresponds to the centroid of the feasibility domain.

Importantly, these figures allow us to provide a theoretical explanation for the positive relationship between evenness and survival probability as follows. As explained in the feasibility analysis section, a vector of carrying capacities located closer to the border of the feasibility domain is more at risk, under demographic stochasticity, of species extinctions. Therefore, it should be theoretically expected that the closer a vector of carrying capacities is to the border of the feasibility domain, the lower will be the average survival probability of the species. Figure 3A represents the same feasibility domain as in figure 2B, where the heat map inside the triangle now shows the average survival probability of species. This figure confirms our theoretical expectation.

Similarly, the closer the vector of carrying capacities is located to the border of the feasibility domain, the lower the level of species evenness (fig. 3B). This is true because at the borders, by definition, one or more species are on the brink of extinction and have very low biomass compared to the others. For instance, the extreme case is when a vector is located at one of the corners of the feasibility domain (blue dots on fig 2B). In that case, one species completely dominates the system and species evenness is close to zero. The heat map inside the feasibility domain of figure 3B shows that as soon as we start moving away from the centroid of the feasibility domain, the level of species evenness starts to decrease. This confirms again our theoretical expectation.

In contrast, figure 3C confirms that there is a very different pattern for community biomass. The figure shows the same representation as figures 3A and B, but this time the heat map inside the triangle corresponds to the relative biomass. This shows that the direction taken from the centroid of the feasibility domain plays an important role in determining the level of community biomass. The community biomass will be maximized (minimized) if the deviation from the centroid moves towards the species with the lowest (largest) average niche overlap. See Appendix E for a mathematical demonstration (available online).

Extending the 3-species illustration to the entire community, figure 4 shows the relationship among deviation from the centroid of the feasibility domain, species evenness, and relative biomass production. First, as expected, the figure shows a clear negative relationship between species evenness and the deviation from the centroid of the feasibility domain. Second, the figure confirms that a high relative biomass production is inevitably associated to a low level of species evenness and a high deviation from the centroid of the feasibility domain. This pattern is highly reproducible in any arbitrarily simulated community of any given size and level of average inter-specific niche overlap (figs. C21-C35, available online).

These findings above confirm that the centroid of the feasibility domain of a niche-competition community (the configuration that allows the largest demographic stress without species extinctions) can only be achieved with high species evenness and an intermediate level of relative biomass. Moreover, these theoretical findings suggest that species evenness can be the result of a fundamental trade-off between species survival probability (or deviation from the centroid of the feasibility domain) and community biomass. In our setting, this trade-off is imposed by the population dynamic. As a consequence, it is not possible to reach a high relative biomass while assuring a low extinction probability in the the community.

Discussion

Previous studies have failed to find a consistent relationship between species evenness and biomass production (see table A2 for a detailed review of the topic, available online).

Our results demonstrate that these mixed outcomes are not idiosyncratic artifacts of different studies, but rather represent equally plausible community trajectories under demographic stochasticity. These trajectories are associated with declining species evenness. They have the largest positive slope in communities that achieve maximal relative biomass production as a result of the low niche-competitive effect of the dominating species on the other species in the community. Conversely, they have a negative slope if the dominant species is in strong competition with the rest of the community. Although there are many ways to be uneven (i.e. different species could dominate to different extents), high evenness requires all species to occur at similar abundances, and this provides more consistent outcomes for persistence and productivity, which can be visualized as the declining variance in survival probability and relative biomass with increasing evenness in figure 1.

There exists some empirical support for our finding that the evenness-productivity relationship should be more positive when the dominant species has a high niche overlap with (i.e. a high competitive effect on) the rest of the community. Nyfeler et al. (2009) found that the evenness-productivity relationship was consistently positive, but its slope declined with added nitrogen (i.e. reduced resource competition). Similarly, studies that compared experimental treatments of tall plants only (high niche overlap) with a mixture of tall and short plants (lower niche overlap) have found more positive evenness-productivity relationships in the high niche overlap treatment (i.e. all plants tall) (Huang et al., 2013; Isbell et al., 2008). This may partly explain previous inconsistencies in the relationship between evenness and productivity found in empirical studies (table A2, available online).

The insurance hypothesis (Yachi and Loreau, 1999) posits that high species richness buffers community responses to perturbation. Superficially, this may suggest that production can be maximized by adding to a single dominant a number of species at low abundance that act as a buffer. In contrast, our results demonstrate that for a given level of species richness, any system dominated by a single or a few species (low evenness) is operating at the brink of extinction of one or more species, such that this buffer will erode over time. Thus, conservation of biodiversity within production systems would appear, from our results, to be least effective when the system is dominated by a single highly-productive species, and diverse plantings may therefore benefit associated self-colonizing biodiversity, as well as production (Erskine et al., 2006).

High species evenness has long been known to characterize natural communities (Odum, 1969), and this has led to its widespread use as a measure of disturbance. We have demonstrated that declining evenness is also a general indicator of further species extinctions, and this result is highly reproducible across different niche-competition communities. As plants are basal species in many food webs, our results raise a number of interesting questions about the extent to which unevenness in plants may indicate decreasing tolerance to perturbations at higher trophic levels, and how declining evenness with increasing perturbation may affect food-web structure by altering species encounter frequencies. An interesting hypothesis would be that disturbance generates low species evenness at multiple trophic levels, and that this would lead to more frequent interactions involving dominant species and the loss of interactions among rare species. Such an hypothesis would be congruent with observed and simulated changes to species interaction networks under global change drivers such as invasion (Aizen et al., 2008), land-use intensification (Tylianakis et al., 2007), changes in interaction strengths (Tylianakis et al., 2008; Saavedra et al., 2013), climate warming and nitrogen deposition (de Sassi et al., 2012), and requires further exploration. Furthermore, we have assumed that species evenness is only a function of changes in demographic characteristics. Future work should also explore the extent to which species turnover, migration, changes in interspecific interactions, and long-term dynamics, among other factors, affect the relationship of species evenness with species survival probability and biomass production. However, these new potential studies should not forget that, without disentangling the competitive effects in these communities, analyses can lead to misleading results.

References

Aizen, M. A., Morales, C. L., and Morales, J. M. 2008. Invasive mutualists erode native pollination webs. PloS Biol 6:e31.

Bastolla, U., L assig, M., Manrubia, S. C., and Valleriani, A. 2005. Biodiversity in model ecosystems, i: coexistence conditions for competing species. J Theor Biol 235:521–530.

Cardinale, B. J., Srivastava, D. S., Emmett Duffy, J., Wright, J. P., Downing, A. L., Sankaran, M., and Jouseau, C. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992.

Case, T. J., 1990. An Illustrated Guide to Theoretical Ecology. Proc Natl Acad Sci U S A.

Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., and Diaz, S. 2000. Consequences of changing biodiversity. Nature 405:234–242.

de Sassi, C., Staniczenko, P. P. A., and Tylianakis, J. M. 2012. Warming and nitrogen affect size structuring and density dependence in a host-parasitoid food web. Philos Trans R Soc Lond B Biol Sci 367:230333041.

Erskine, P. D., Lamb, D., and Bristow, M. 2006. Tree species diversity and ecosystem function: can tropical multi-species plantations generate greater productivity? For Ecol Manage 233:205–210.

Halloy, S. R. P. and Barratt, B. I. P. 2007. Patterns of abundance and morphology as indicators of ecosystem status: A meta-analysis. Ecological Complexity 4:128–147.

Hector, A. and Bagchi, R. 2007. Biodiversity and ecosystem multifunctionality. Nature 488:188–190.

Hillebrand, H., Bennett, D. M., and Cadotte, M. W. 2008. Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. Ecology 89:1510–1520.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., LAvorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A. J., Vandermeer, J., and Wardle, D. A. 2005. Effects of biodiversity on ecosystem functioning: a consenus of current knowledge. Ecol Monogr 75:3–35.

Huang, Y., Martin, L., Isbell, F., and Wilsey, B. 2013. Is community persistence related to diversity? A test with prairie species in a long-term experiment. Basic and Applied Ecology 14:199–207.

Huston, M. 1979. A general hypothesis of species diversity. Am Nat 113:81–101.

Isbell, F. I., Losure, D. A., Yurkonis, K. A., and Wilsey, B. J. 2008. Diversityproductivity relationships in two ecologically realistic rarityextinction scenarios. Oikos 117:996–1005.

Laliberté, E., Lambers, H., Norton, D. A., Tylianakis, J. M., and Hustonand, M. A. 2013. A long-term experimental test of the dynamic equilibrium model of species diversity. Oecologia 171:439–448.

Levins, R., 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press, USA.

Logofet, D. O., 1993. Matrices and Graphs: Stability Problems in Mathematical Ecology. CRC Press.

Loreau, M. 1998. Separating sampling and other effects in biodiversity experiments. Oikos 82:600–602.

Loreau, M., 2010. From population to ecosystems: theoretical foundations for a new ecological synthesis. Princeton University Press, Princeton.

MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am Nat 101:377–385.

Margalef, R. 1963. On certain unifying principles in ecology. Am Nat 97:357–374.

Margalef, R., 1968. Perspectives in Ecological Theory. University of Chicago Press.

Mulder, C. P. H., Bazeley-White, E., Dimitrakopoulos, P. G., Hector, A., Scherer-Lorenzen, M., and Schmid, B. 2004. Species evenness and productivity in experimental plant communities. Oikos 107:50–63.

Nijs, I. and Roy, J. 2000. How important are species richness, species evenness and interspecific differences to productivity? a mathematical model. Oikos 88:57–66.

Norberg, J., Swaney, D. P., Dushoff, J., Lin, J., Casagrandi, R., and Levin, S. A. 2001. Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. Proc Natl Acad Sci U S A 98:1137611381.

Nyfeler, D., Huguenin-Elie, O., Suter, M., Frossard, E., Connolly, J., and Lüscher, A. 2009. Strong mixture effects among four species in fertilized agricultural grassland led to persistent and consistent transgressive overyielding. Journal of Applied Ecology 46:683–691.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.

Preston, F. W. 1948. The commonness, and rarity, of species. Ecology 29:254–283.

Rohr, R. P., Saavedra, S., and Bascompte, J. 2014. On the structural stability of mutualistic systems. Science 345:1253497.

Saavedra, S., Rohr, R. P., Dakos, V., and Bascompte, J. 2013. Estimating the tolerance of species to the effects of global environmental change. Nat Commun 4:2350.

Saavedra, S., Rohr, R. P., Fortuna, M. A., Selva, N., and Bascompte, J. 2016*a*. Seasonal species interactions minimize the impact of species turnover on the likelihood of community persistence. Ecology 97:865–873.

Saavedra, S., Rohr, R. P., Gilarranz, L. J., and Bascompte, J. 2014. How structurally stable are global socioeconomic systems? J R Soc Interface 11:20140693.

Saavedra, S., Rohr, R. P., Olesen, J. M., and Bascompte, J. 2016*b*. Nested species interactions promote feasibility over stability during the assembly of a pollinator community. Ecology and Evolution doi:10.1002/ece3.1930.

Stirling, G. and Wilsey, B. 2001. Empirical relationships between species richness, evenness, and proportional diversity. Am Nat 158:286–299.

Sugihara, G., Bersier, L.-F., Southwood, R. E., Pimm, S. L., and May, R. M. 2003. Predicted correspondence between species abundances and dendrograms of niche similarities. Proc Natl Acad Sci U S A 100:52465251.

Svirezhev, Y. M. and Logofet, D. O., 1983. Stability of Biological Communities. Mir Publishers.

Tilman, D., Wedin, D., and Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720.

Tokeshi, M. 1990. Niche apportionment or random assortment: species abundance patterns revisited. J. Anim. Ecol. 59:1129–1146.

Tylianakis, J. M., Didham, R. K., Bascompte, J., and Wardle, D. A. 2008. Global change and species interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363.

Tylianakis, J. M., Tscharntke, T., and Lewis, O. T. 2007. Habitat modification alters the structure of tropical host. Nature 445:202–205.

Vandermeer, J. H. 1970. The community matrix and the number of species in a community. Am Nat 104:78–83.

Vellend, M., Baeten, L., Myers-Smith, I. H., Elmendorf, S. C., Beauséjour, R., Brown, C. D., De Frenne, P., Verheyen, K., and Wipf, S. 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. Proc Natl Acad Sci U S A 110:19456–19459.

Volterra, V., 1931. Leçons sur la théorie mathématique de la lutte pour la vie. Gauthier-Villars, Paris.

Wardle, D. A., Zachrisson, O., Hörnberg, G., and Gallet, C. 1997. The influence of island area on ecosystem properties. Science 227:1296–1299.

Wilsey, B. J. and Potvin, C. 2000. Biodiversity and ecosystem functioning: Importance of species eveness in an old field. Ecology 81:887–892.

Wittebolle, L., Marzorati, M., Clement, L., Balloi, A., Daffonchio, D., Heylen, K., De-Vos, P., Verstraete, W., and Boon, N. 2009. Initial community evenness favours functionality under selective stress. Nature 458:623–626.

Yachi, S. and Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proc Natl Acad Sci U S A 96:1463–1468.

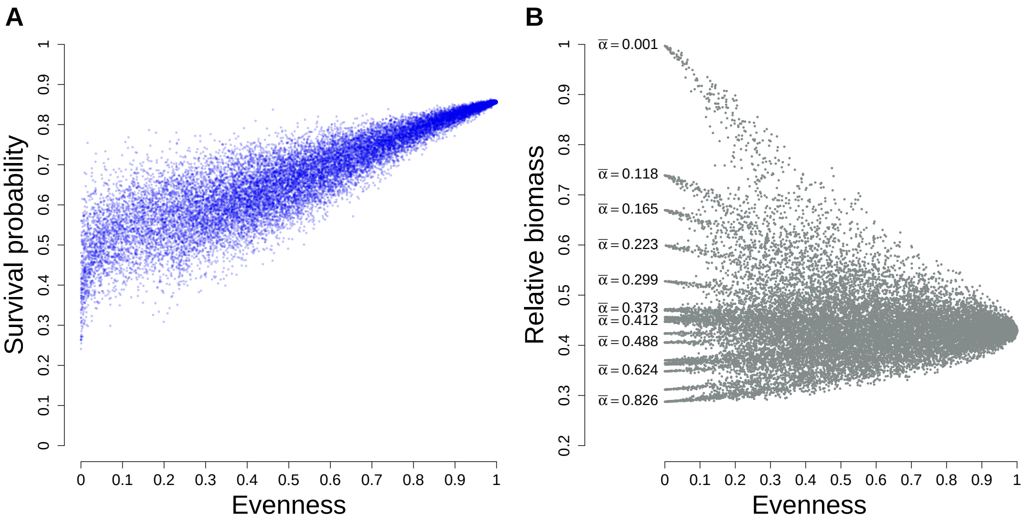

Figure 1: **Association of species evenness with average survival of species and relative biomass.** This figure corresponds to a randomly-generated niche-overlap matrix of 20 species and an average inter-specific niche overlap of 0.07 (see Methods). Each point represents a randomly-generated distribution of species biomass given a niche overlap matrix. Panel **A** shows a strong positive relationship between species evenness and average survival probability of species under demographic stochasticity. The standard deviation of the stochastic noise was chosen equal to 0.1. Panel **B** shows that reducing species evenness in the community can result in either increases, no change, or decreases in relative biomass. This direction depends on whether the community is dominated by a species that engages in an average low or high niche competition ($\bar{\alpha}$). This pattern is highly reproducible in any arbitrarily simulated community of any given size (see Online Material).

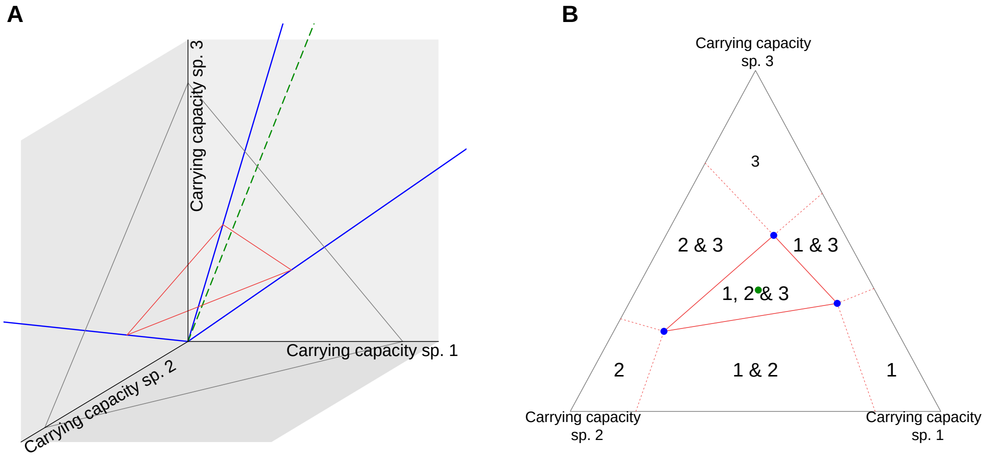

Figure 2: **Graphical representation of the feasibility domain.** Panel **A** corresponds to the projection of the community shown in fig. 1 on a subset of three randomly chosen species. The three black axes represent the full domain of carrying capacities. The angle formed by the three blue lines corresponds to the algebraic cone of the feasibility domain, i.e., the subset of carrying capacities leading the positive biomass for the three species at the stable steady-states of the Lotka-Volterra model. The dashed lines in the middle (green) corresponds to the centroid of the feasibility domain (structural vector). To simplify the representation of the feasibility domain, we can take a slice of the full domain. This slice is represented by the outer gray triangle. The red inner triangle is the corresponding slice of the feasibility cone. Panel **B** is a 2-dimensional representation of the slice of panel **A**. The outer gray triangle is split into 7 domains. The inner red triangle represents the feasibility domain (the three species have positive biomass at equilibrium), while in the other six domains at least one species goes extinct. The identity of the surviving species is given by the numbers inside the domain. Note that the slice is the projection of the full space on the unit simplex, i.e., where the sum of the carrying capacity is equal to one. Therefore, the slice is a complete representation of carrying capacities space up to a scaling factor.

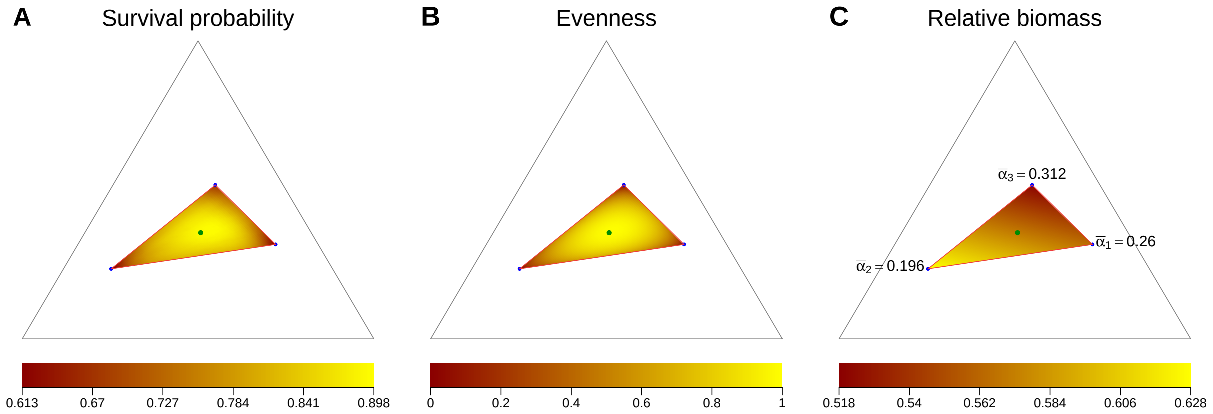

Figure 3: **Linking species survival probability, community evenness, and biomass production** Panels **A**-**C** represent the same 2-dimensional slice of the cone describing the feasibility domain in Fig. 2. The heat maps inside the inner triangle correspond to the levels of average survival probability, species evenness, and relative biomass, respectively. The figure shows a positive correlation between survival probability and evenness, while the relationship between community evenness and relative biomass is multidirectional.

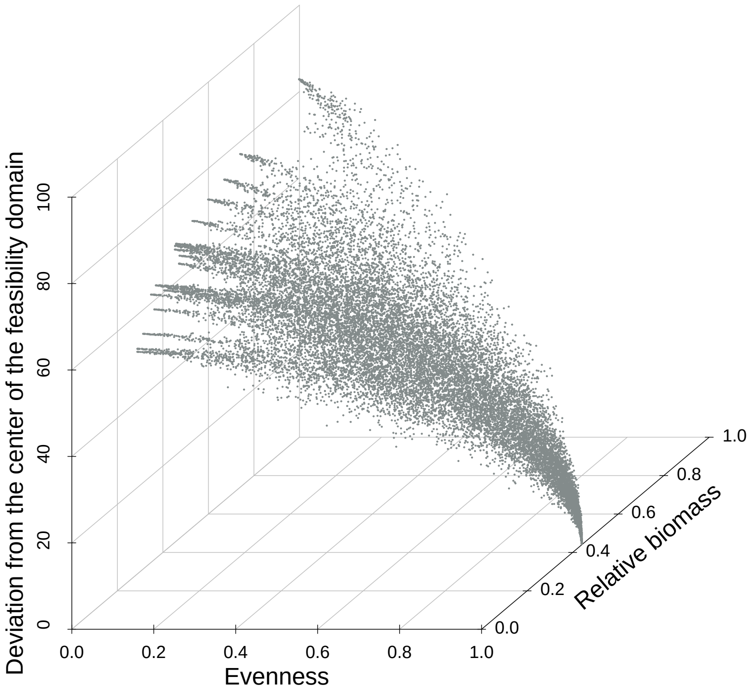

Figure 4: **Disentangling the effects of species evenness and biomass production on species survival.** The figure shows the relationship among deviation from the centroid of the feasibility domain, species evenness, and relative biomass for the full community shown in Fig 1. The larger the deviation is, the lower the average species survival probability under demographic stochasticity. This illustrates that both species evenness and relative biomass production are the result of a given level of deviation of the community from the centroid of its feasibility domain. Each point represents a randomly-generated distribution of species biomass. This pattern is highly reproducible in any arbitrarily simulated community of any given size and level of average niche overlap (figs. C1-C7, available online).